Distribution, dispersion and regulation in a population of the Common Shelduck

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Introduction

This paper arose from a wider study undertaken to evaluate changes in the population of the Isle of Sheppey, Kent, since a previous study, (Hori 1964 and 1969). It became evident that the behaviour of groups in nesting areas and multiple nesting were more important than had been previously considered. These aspects were subjected to closer study and compared with results from the previous work, limited data from other years and other published results (Jenkins *et al.* 1975; Patterson 1982; Pienkowski and Evans 1982a and b).

Methods

Field-work was undertaken between October 1983 and September 1986, on alternate days from early February until late August in each year and twice weekly in other periods. Generally this occupied 12–15 hours a day from February until June and 8–10 hours at other dates. From February until August it began just before first light. All times given are GMT.

Methods were those used previously (Hori 1964, 1969), augmented by increased mobility, using a 4 wheel drive Jeep which doubled as a mobile hide; prolonged behaviour studies of individuals; monitoring of communes and the intensive study of one; colour ringing of incubating females and detailed recording and recognition of facial descriptions in particular groups and locations; more use of the fact that females "in lay" often show prominent egg bulges on the lower belly, and laying can often be deduced by the individuals' appearance before and after nest visits.

In the detailed study of one commune additional methods included marking, measuring and weighing eggs; determination of females' presence on the nest through their hissing reactions and continuous recording of behavioural activity. All these nest sites were in a stack of straw bales in a concrete framed barn clad with corrugated asbestos on the roof and ends. The sites may be considered as modified versions of those which have long been used by Shelduck in North Kent. In such situations birds have used gaps left accidentally or which develop as the straw stack settles. Artificial sites were made by re-stacking bales to provide approach tunnels, nesting chambers, and hiding tunnels as previously described (Hori 1964). A bale above the nesting chamber was arranged for quick removal so that incubating birds could be easily caught later. Obviously such sites had to be near the top of the stack, but this was in any case preferred by Shelduck. All other holes in the stack were blocked to prevent birds nesting in inaccessible situations.

The size of the nesting chamber was always a compromise between the preference shown for small chambers and the possibility that the nest might have become a multiple site. This was usually accommodated by keeping approach tunnels small so that the bird could only just get in, but providing more space in the chamber. Provision was made for a shielded landing space near hole entrances, by forming a large open-sided well in the stack which screened the nest holes on three sides, but allowed observation at the other.

Field Studies

The Environment

Sheppey lies along the North Kent littoral, separated from the mainland by the Swale channel, the foreshore and main creeks of which provide primary winter feeding (Figure 1). Land in the area frequented by Shelduck (which does not include the Thames shore) is predominantly used for farming, although reserves operated by the Royal Society for the Protection of birds (RSPB) and the Nature Conservancy Council (NCC) now occupy significant areas. During the sixties study some 3,700 hectares of this area was fresh grazing marsh, but now only approximately 1,800 hectares remains, nearly all in the reserves. The rest has been drained and turned over to cereal

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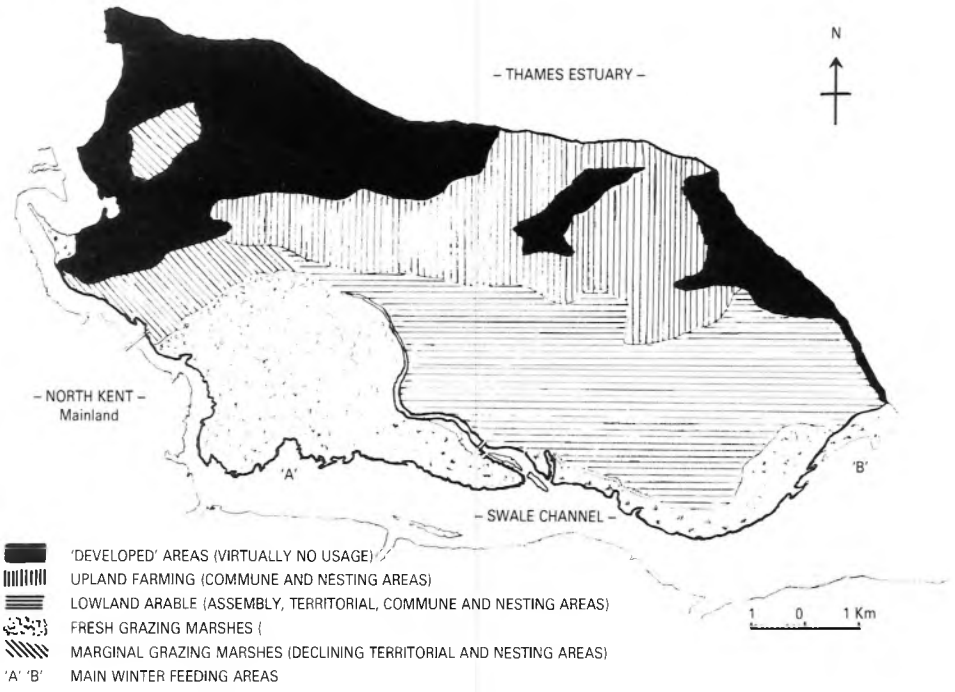


Figure 1. Map showing Shelduck habitats on the Isle of Sheppey, Kent.

and other cash crops. Dutch Elm disease had killed off *Ulmus procera* and most of their remains had been removed by 1980. These had been the common hedgerow tree and their loss modified the landscape importantly.

Dispersion

Separation out of the breeding population begins early in February. It is complex, with considerable variation in behaviour and with birds reaching different stages in the sequence at different times. Pairs differ in experience, social preferences, and feeding, territory and nesting area preferences, making overall statements difficult. The island does not have areas where some pairs breed in isolation and others in colonies as reported by Pienkowski and Evans (1982a) for the Firth of Forth.

For most potential breeders there is progressive movement away from the Swale channel, the winter habitat, as follows:-

(i) From about the beginning of February the whole population spent increasing time on the fresh marshes, generally on or near water.

(ii) The potential breeding population separated from the remainder. For most there was a distinct physical separation, sometimes only a score of metres or less, but others, in "overlap areas", continued to use flood water with non-breeders.

(iii) At about the same time, smaller groups appeared in the grazing marshes and arable; territories started to be occupied. Those along the shore were occupied first, particularly in protected creeks. The limiting factor appeared to be disturbance by shore shooting. Directly this ceased, territorial behaviour was detected. Territories on fresh water, the majority, were occupied later. Fresh water was frozen most mornings until the end of February or early March. In severe weather first occupation of shore and fresh water territories differed by nearly a month.

(iv) After a period of territorial occupation, groups, called 'communes', began to occur in nesting localities. The time lapse before birds began visiting nesting areas varied from 7 to 32 days.

Behaviour in (iii) and (iv) differs from that reported for the Ythan by Williams (1973), where pairs visited nesting areas before, during and after taking up territory.

By the time dispersion of the breeding population had occurred, residual wintering birds had left and the non-breeding population was largely concentrated in two areas near the shore.

Expansion of area in which territories occur

On Sheppey and in other parts of the North Kent Marshes, Shelduck have adapted to fresh water territories. This probably resulted from reclamation, when sea defences transformed tidal channels into fresh water fleets. The change would have taken some years, with a transition through brackish conditions and adaptation would have been facilitated by the diet flexibility exhibited by Shelduck in spring and summer. Ringed pairs holding territory on fresh water were regularly observed feeding on tidal mud up to 3 km away during incubation, and territorial pairs on fleets often fed in other locations, such as freshly sown fields when foraging for seed.

Groups in nesting locations

These groups may be regarded as the penultimate stage in the sequence of dispersion. They were termed communes earlier (Hori 1964 and 1969). To prevent misunderstanding, an extended definition of communes is considered necessary, namely "Groups of adult pairs, all potential breeders, which assemble in the same location near nesting sites each morning after territories had been established, but before nest prospecting commenced; from April to approximately the second half of May. These groups continue through the prospecting period, but wane quickly at the onset of laying, though some members of the group may associate well into incubation". Colour ringing confirmed numerical evidence that the groups contained the same birds, apart from mortality, and that individuals returned to the same communes in succeeding years. The addition of dates allows for the discovery, in the present study, that communes can be joined later in the season by further groups of adults. Similar groups have been detected in other studies, notably by Patterson and Makepeace (1979) and Patterson (1982)

Patterson suggested that they are synonymous with groups which Young (1970) called "Parliaments", presumably after Coombes, (in Huxley 1951), and that the term "sub-group" be used instead of either of the somewhat anthropomorphic names. This suggestion is not adopted here because it introduces vagueness unless the various sub groups which occur in breeding populations are defined and given suffixes or prefixes, e.g. "nesting locality sub-group".

The study of Sheppey communes was facilitated by the fact that those in the uplands and some in the arable were virtually isolated. Interference and confusion caused by non-breeding birds was minimal. In the sixties study such intrusion was unknown, but it was observed on a number of occasions in the eighties and is expected to increase.

Table 1. Commune numbers and locations

	1984	1985	1986
Total of communes found	38	39	35
Upland communes included	21	21	21
Total adult pairs in communes	148	139	169

Table 1 shows the numbers and sub-location of communes in the eighties. These groups were not entirely exclusive and some pairs moved between them.

Sixteen upland communes were recorded between 1960 and 1966 and had been known individually to farmers and farm workers for more than thirty years before. Nine of these remained in precisely the same locations through the eighties' study so they had persisted for more than fifty years. The others had moved only because of major land usage changes, including destruction of nesting sites.

Tendency of inexperienced birds to follow experienced ones

Non-breeders indulge in apparently aimless prospecting of holes. Large groups of non-breeding pairs, up to 24, gather near burrows or other sites and spend long periods displaying and running in and out of holes which are not used for nesting. This may be part of a learning process which reinforces an innate tendency to recognize holes as

nesting places. Non-breeding pairs were predominantly immature females with adult mates, a result of the excess of males in both summer and winter populations. Pairing display flights confirmed this. The process of pairing keeps such pairs longer in the wintering areas. Movement of non-breeding pairs into other areas was most apparent in May and June, as was also reported by Patterson and Makepeace (1979), but some began to follow adult pairs earlier when the latter moved to territories near, or overlapping, winter areas. Later, some even followed as far as the upland communes.

The same tendency to follow occurred in the breeding population; it was most apparent away from areas where non-breeders overlap. As the breeding population separated, experienced adults returned to territorial and subsequently to commune areas first. There was a short delay before other pairs in adult plumage followed experienced adults to territorial fleets, and associated with them in small groups. The inexperienced birds continued to group whilst experienced pairs consolidated territories. When experienced birds began to visit commune areas there was another time lapse, e.g. 8–10 days, before the inexperienced birds began following. In both flights to territory and to communes, pairs were seen taking off, flying and landing closely behind others in hundreds of instances. Following could have been minimised if experienced adults made their way from territories to commune areas directly and discreetly during the initial and prospecting periods, as they do for most of the laying and all of the incubation periods. Instead, commune groups are obvious and form well before laying commences, even before prospecting starts. This facilitates following, with the consequent transfer of information on nesting areas and ultimately of nest sites.

Individual and multiple nests

Nests occur throughout the undeveloped land and into the fringes of development (Figure 1), with a definite tendency to be clumped. Nests were single, i.e. laid and incubated by one female, or multiple, i.e. laid by a number of females, but incubated by only one. The approximate criterion that clutches larger than 12 eggs were multiples (Hori 1969) was used where there was uncertainty, but this proved to be an underestimate occasionally.

In 189 completed clutches examined in both studies the average clutch size for 137 single nests was 9.05±0.14 eggs, with a mode of 10. Multiple clutches in which laying was completed, are shown in Table 2. In 1986, 2 additional nests with less than 12 eggs were clearly multiple. The significance of multiple nesting is best illustrated by the proportion of pairs and of eggs laid, as shown in Table 3.

Previous studies attempted to supplement such data with those obtained from class I duckling broods (Hori 1964 and 1969). In 1984–86 inclusive, further efforts were made to intercept broods en route to nurseries. Such counts were not, however, considered satisfactory because they do not give data on nest losses, depressed hatching success and early duckling losses.

Table 2. Multiple clutches

Year	Multiple Nests	Nests containing number of eggs shown 13	14	15	16	17	18	>18
1962	3	1	–	–	–	–	1	1x20
63	12	2	3	3	–	1	1	1x22, 1x25
64	3	–	–	–	–	1	–	2x19
65	2	–	1	1	–	–	–	–
66	6	–	1	2	1	–	–	1x21, 1x23
67	5	–	2	–	1	1	–	1x32
68	3	1	–	–	1	–	–	1x23
1984	3	–	–	–	1	–	–	1x24, 1x26
85	6	–	–	1	–	1	–	1x20, 1x21, 1x24, 1x25
86	8	1	1	–	1	1	1	1x20, 1x25, 1x31
Total	51	5	8	7	5	5	3	18

Table 3. Incidence of multiple nesting.

	1962	63	64	65	66	67	68	84	85	86
Total nests	13	25	22	19	25	13	13	17	22	20
Multiple nests	23%	48%	14%	11%	28%	38%	23%	18%	27%	50%
Total eggs in sample	127	315	228	181	213	131	119	108	229	253
Pairs using multiple nests	47%	50%	32%	26%	56%	47%	31%	39%	56%	77%
Eggs in multiple nests	40%	62%	24%	16%	21%	47%	24%	48%	54%	61%

Work on the Ythan (Patterson 1982) and on the Firth of Forth, (Pienkowski and Evans 1982b) suggested that burrows in soft sand often collapse: a hazard which would be increased in multiple nests by the passage of additional birds. Such unstable sites were seldom encountered on Sheppey; there was one case in loose straw. Site constraints did not influence multiple laying. Eggs were piled in layers in deep sites or formed long rows in narrow ones. Where it was possible for a bird to cover the eggs and to rearrange them, large multiple clutches were hatched. For example, a complete hatch of 19 was achieved in 1985 in a disguised tea chest where the eggs were arranged in a single layer. The same bird could not, however, manage 30 eggs in the same site in 1986. There was not even enough down to cover the eggs when she left the nest, and all failed. No traces of embryo development were found in the eggs, which were incubated for 44 days.

Comparative hatching success is shown in Table 4. Widely different hatching figures obtained for multiple nests in the sixties and the eighties are apparent. Evidence that nesting was generally more difficult in the eighties was corroborated by the lower success rates also found in single nests.

Only once was a female known to react to the number of eggs laid. In 1985 this bird separated out a group of 8, then after they had been restored to the clutch, separated a group of 13, from 25 eggs laid in a multiple nest. Eggs laid near clutches were always ignored, as were those which became accidentally separated from clutches. Ejection of eggs reported by Pienkowski and Evans (1982b) was not experienced.

A total of 21 single eggs and two lots of 2 eggs were found near clutches. They were usually found in approach tunnels and occasionally beyond clutches. During the earlier work, birds were seen sitting near others which were on clutches, and it is considered that the presence of a sitting bird usually causes eggs to be so laid. Many other singles, noticeable by their shape and size were laid in the clutches. Rarely such eggs were found in otherwise empty sites.

During laying, some partially completed clutches were covered with loose material when the bird left. This occurred in 51% of a sample of 43 nests in the earlier study, and 75% of 24 nests in the present study. The availability of loose material, usually straw or wood litter, obviously affects the habit. This behaviour could be hiding eggs, rather than insulating them which is the primary purpose of the down cover used during incubation. Hiding could reduce multiple laying. Multiple nesting may lead to dump nesting in which so many eggs are laid that it is impossible for a bird to incubate them, e.g. 50 Isakov (1952), 32 (Hori 1969), 31 (this study). The disruption caused by the numbers of birds involved also virtually precludes the possibility of successful incubation, but some birds attempt it.

Table 4. Comparative hatching success (% eggs hatched/laid) in single and multiple nests.

	1963	64	65	66	67	68	84	85	86
No. of single clutches	8	12	9	8	6	10	14	14	6
Hatching success	90%	93%	87%	92%	88%	N/A	37%	64%	65%
No. of multiple nests	8	2	2	6	3	3	3	6	10
Hatching success	91%	95%	90%	89%	85%	N/A	27%	37%	25%

Detailed study of one commune

Almost ideal study conditions occurred in 1986 at an upland farm where communes had been observed generally in eleven of the years since 1962. This group was studied intensively for 46 days, usually on alternate days, but consecutively when necessary. Observation periods averaged approximately 3 hours, but varied up to 8¼ hours. The assembly area had always been the same hillside pasture, and nests were centred on a barn variously stacked with hay or straw bales. Three to six nests were made here annually, with up to four in the barn. In some years some pairs nested in other sites up to 400 m from the assembly ground. Fifteen incubating females were ringed here in the sixties, but none of these were seen during the eighties. Figure 2 shows details of the location and Figure 3 the entrances to the nests. The latter were 3.5 to 5 m above the ground. Observations began at, or before, first light. Nest checks were made after morning behaviour studies. During incubation this necessitated discovering when females were usually absent. All nests were in sites prepared as stated in Methods.

Recognition of young and inexperienced females

The breeding biology of females from age two to maturity has not yet been elucidated. Ringing of ducklings or yearlings, followed by later territorial and nest studies would be the only reliable method. In this study less positive methods were used. No consistent field characters were discovered; commune birds frequently showed pale or greyish legs, but some incubating females also had such legs when they had virtually fully adult wing plumage. Facial markings of adult females varied but some apparently young females have no conspicuous face markings, whilst some incubating adults have faces almost identical to the juveniles.

Of the incubating females caught 72 were fully examined in the hand. Of these only 4 had no white edges to primary and secondary feathers and pure white greater coverts. The majority, 52, had small amounts of white edging or speckling on the flight feathers, typically 0.5 – 3 mm tips on some primaries and secondaries. Whether this should be expected in fully mature birds is uncertain. There is sufficient anomaly in

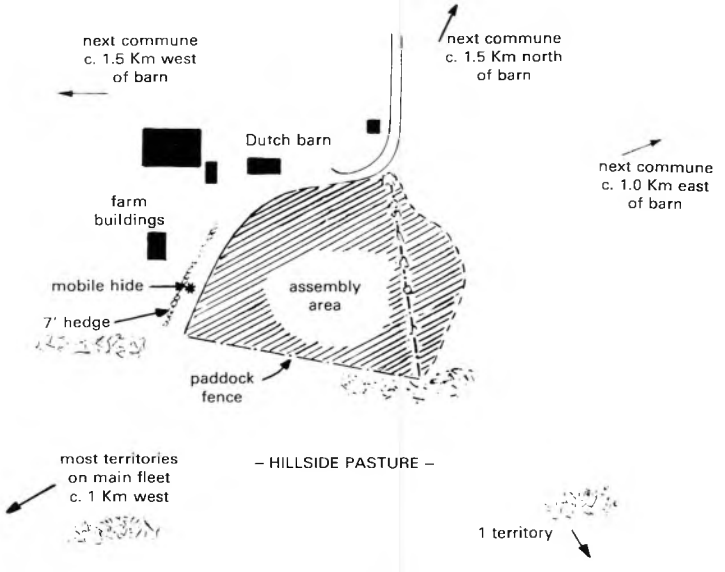
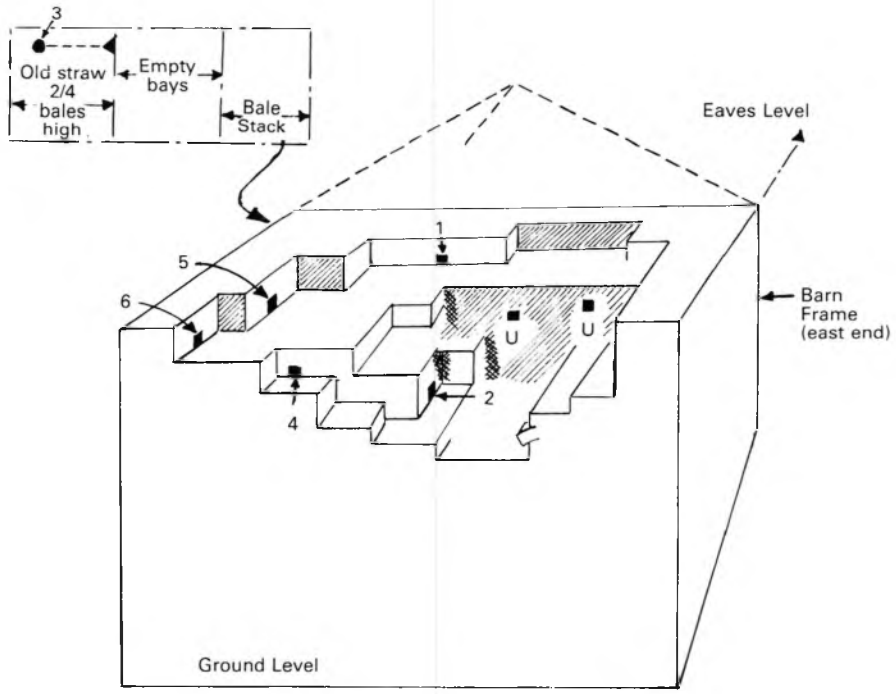


Figure 2. Plan of upland commune site subjected to close study in 1986.

Figure 3. Diagram of straw stack in Dutch barn (Figure 2) showing nest entrances.



published descriptions to raise doubt on the extent to which age was known. However, more pertinent for present purposes was the fact that the other 20 birds had small grey tips to some greater coverts as well as the white tips to flight feathers. In two cases there were prominent dark grey covert tips. These were considered to be young adults, at minimum, aged two.

From behaviour studies in communes, on territories and in other assembly areas, it was concluded that inexperienced birds could usually be differentiated from mature breeders in the breeding season by behaviour. Such immature behaviour included:-

- remaining in groups on or near occupied territories and moving with such groups away from the territories while experienced birds remained there
- appearing at territorial and commune areas later than experienced birds
- involvement in protracted group displays on commune assembly areas, particularly near nest sites
- following experienced pairs to and on commune areas
- visiting nest sites in groups and staying for long periods, associating and displaying
- showing greater timidity in approaching and entering nest sites and inspecting various holes for very short periods without laying
- not showing avoiding behaviour as the laying period approached, nor varying visit times
- forming densely packed flocks on the grazing marshes, often still displaying in groups, as late the third week in May
- not making low direct flights when moving from territorial or other areas to nests.

Individuals involved

Twenty pairs visited this location in two phases. A lone drake and a pair with an immature female were seen only once and were not considered to have taken an active part in nesting. Five pairs had colour ringed females, whilst 12 of the others had recognisably different females, although three of these could only be separated when seen

together. Their background and status are shown in Table 5.

Four pairs, including one with a ringed female, first visited the pasture on 1st April; subsequently called Day 1. This was 25 days after first arrivals in the corresponding territory areas. However, the latter were in groups and territorial occupation was not proved until 14 days before Day 1. April 1st was approximately normal for this group and 21 days after the first upland commune on the island assembled. Activity then continued until Day 99 (8th July). This duration was unprecendented.

Visit times and durations corresponded overwhelmingly with minimum human activity, from around first light to commencement of farm work. Periods varied from approximately one hour at Day 1 to three hours at the beginning of laying, as day length increased.

Sequence of behaviour

Behaviour in communes develops through a sequence of activities until, during laying and especially during incubation, experienced birds visit nests with considerable stealth and are only briefly seen. In this commune the sequence was divided into arbitrary periods:-

(a) Initial period: Day 1 to Day 22 (1st–22nd April)

This covers the period up to the day on which a pair first visited the barn. Initially, behaviour comprised mainly feeding and sleeping, but sitting or standing alert, "walking up" and inter-pair display gradually increased (see Hori 1964; Patterson 1982). At first pairs appear to seek only group association in the nesting location, but alert postures suggest that they are

Table 5. Individual histories of Shelduck in the closely studied commune.

Rings	1984	1985	1986
Blue/yellow	Not known.	Ringed on nest in barn. Hatched all of 11 eggs. Fully adult plumage.	Laid, incubated and deserted multiple nest 1.
Green/yellow	Ringed on nest in barn. Clutch of 11 eggs predated. Fully adult plumage.	Seen in commune and at barn. Not caught	Laid in and incubated multiple nest 2. Hatched 13 of 16 eggs.
Black/white	Ringed on multiple nest (16 eggs) in barn. Deserted after disturbance by farm-work. Fully adult plumage.	Not seen.	Laid initially in nest 1. Moved to nest 3 and hatched 9 of 13 eggs.
White/blue	Not known.	Ringed on multiple nest in barn. Hatched 16 of 21 eggs. Fully adult plumage.	Laid in nest 1 and 2. Incubated nest 4, hatched 10 of 20 eggs.
Orange/blue	Not known.	Ringed on nest in straw dump 400 m west of barn. Hatched all of 11 eggs.	Visited all nests. Competed for nest 2 but excluded. Probably also laid in nests 3 and 4. Did not incubate, last seen Day 57.
Yellow/red	Not known.	Not known.	2nd phase bird. Incubated small multiple clutch (10 eggs). Returned to wrong nest after ringing. Traces of immature plumage.

registering all aspects of the location.

Initial visits were short, approximately 1 hour, but sometimes as short as 12 minutes. Bad weather precluded them altogether, e.g. during blizzards and extreme cold with high winds, there were only two visits between Days 8 and 11. At first a shepherd checking the lambing flock would cause all pairs to fly back to territories, but increasingly they tolerated disturbance and merely retreated into the pasture. This parallels the behaviour on territories where, when well established, pairs often merely fly round a person walking along a fleet.

Some pairs arrived before first light, approximately 04.50 to 04.15 but most came soon after. Daily totals increased from 4 to 9 pairs. The birds gradually moved nearer to the barn: the nearest approach during this period was 30 m. It was difficult, sometimes impossible, to determine the extent to which birds were associating from preference, or could not avoid it. "Walking up" was a particular behaviour in which pairs moved towards the barn from 100/150 m out in the pasture. It was purposive, with birds often displaying at low intensity to each other, but interspersed with periods of feeding, resting and sleeping, and inter-pair display. Males and females were almost equally leaders. By the end of the period birds stayed in the commune up to 3½ hours.

(b) 1st Phase nest prospecting: Days 23 to 33 (23rd April to 3rd May)

The first stack visit seen was by a ringed female on Day 23: she landed at the foot of the stack, but did not go on it. Subsequently, increasing numbers went into the stack until most prospected it on Day 32: on that day there were 18 birds on the straw at one stage. At least one marked bird, orange/blue, had already prospected another location, 400 m to the west, where it nested the previous year, but this had been completely cleared of straw and offered no possibility of a nest site.

By Day 23, pairs only retreated 80–100 m into the pasture when farm workers arrived and returned within a few minutes of disturbance. They returned up to five times following repeated disturbance between 07.00 and 10.00.

Feeding, resting/sleeping and "walking up" decreased markedly. The latter because birds arriving from territories landed nearer the barn as the period progressed. Group display more than doubled, noticeably by birds considered inexperienced. Experienced birds repeatedly distanced themselves from display groups and sat or stood watching: they became alert when others visited certain holes. Five pairs with ringed females were present in the group at this time. Experienced pairs began to show violent aggression towards other pairs near the stack. This was noticeably different from the chasing and threatening lunges used in group display.

Two ringed females were first seen with large egg bulges on Day 32. One of these was seen leaving a nest without an egg bulge the next morning and the first egg found there was considered hers.

(c) 1st Phase laying: Day 34 to Day 58 (3rd May to 28th May)

The next 24 days ecompassed egg laying by the first stage commune. Females, known to be experienced, tried increasingly to distance themselves from others. Stack visits increased until experienced birds visited at least once and others, considered inexperienced, three or four times per morning. The latter also followed others and formed groups on the stack. Experienced birds began to vary their visit times. It appeared that they had also learned to avoid farm workers by this date. After Day 49 such birds were seldom seen in the early morning groups. Some laying pairs seized opportunities to visit the stack unnoticed. Repeatedly, after a group had been disturbed by farm workers, and as soon as quiet had returned, a ringed female and her mate would appear as from nowhere and fly or run to the stack. Occasionally such pairs, ringed and known to be laying, would notice another pair following them and would turn on them with extreme aggression, driving the followers from the pasture. Some experienced birds arriving from territories flew direct to the stack, with females going into it and males veering away at the last moment, giving a visible presence at the stack of only a few seconds.

Progress in the nests was as follows:-

Nest 1. From the start of laying until the start of incubation (Days 33 to 45), four different females were seen to visit, but probably at least six did so. Two experienced birds, Blue/yellow and Black/white were seen most often. The females saw each

other visit the nest and both were excluded from it by others more than once. Black/white first prospected it, but Blue/yellow was considered to have laid the first egg; Black/white was not seen with an egg bulge until Day 36.

Although three females were visiting the nest between Days 33 and 42, and two were heavily in lay, only one egg a day was laid. This and many other cases of delayed, interrupted and extended laying were recorded through the studies and remain difficult to explain. In some cases interruptions resulted from desertion and subsequent continuation by other birds, but in others the same bird or birds were involved. Either females can retain eggs low down in the reproductive tract for longer than is usually supposed, or the eggs must be deposited elsewhere. Birds repeatedly tried to get to nests over long periods, for example through most of a day, when farming activity occurred near a nest site; so eggs can be retained. On the other hand egg dropping has been regularly reported (e.g. Hori 1964; Young 1964). Territories were searched systematically, but no eggs were found in this study.

On Day 40 Black/white moved to another site, nest 3. Two birds continued laying in nest 1 and at least two others laid near it. At least one female completely covered the clutch with straw when she left. An unringed female commenced incubation on Day 45 when there were 17 eggs, but laying continued. Blue/yellow continued to visit and remained visibly in lay.

There was considerable interference between Days 41 and 49. For example, on Day 46 when Blue/yellow fluttered up to the nest her mate left her and flew back to territory. In this case Blue/yellow could not get on the clutch and came out immediately. She spent the rest of the observation period standing near other pairs, watching the site. Sometime between Days 46 and 49 inclusive, she took over the incubation.

Three more eggs were laid after incubation started. One as late as Day 73. Similar late deposition of eggs was noted in a number of cases throughout the studies. Many such eggs have no chance of hatching, e.g. one laid 18 days after the start of incubation in this case.

Nest 2. At least two females, both ringed, visited this nest during the first days of laying, which started on Day 37. As in nest 1, only one egg a day was laid for the first thirteen days. Green/yellow, who incubated, was only seen twice in the early mornings during laying and visited at other times; she was only seen once with an egg bulge. By contrast, the other main competitor, Orange/blue, showed egg bulges between Days 39 and 57 inclusive and visited all the first four nests during the laying period in Nest 2.

Green/yellow started incubation of 11 eggs on either Day 46 or 47. Two more eggs were laid during the next two days; one by Orange/blue and one by an unmarked bird. Subsequently, 3 more were laid on Days 51, 57 and 63. Orange/blue was considered to have laid the egg on Day 51, but the last two were by others.

Although tolerant of disturbance, Green/yellow was not immune to it. She flew off the nest of Day 51, leaving the clutch uncovered, when an intruding bird was expelled from nest 4, immediately above, with a considerable clamour. At the time, i.e. 11.40, she had been incubating since 03.45.

Nest 3. Black/white began this clutch on Day 40 after leaving nest 1, in which she laid at least 1 egg. On Day 42 there were 3 eggs after she had spent 52 minutes on the nest. Only 2 eggs were laid in the next 5 days, but thereafter there was daily laying until Black/white commenced incubation of 8 eggs on Day 50. Four more eggs were laid during the next 6 days, at least one by Orange/blue, the bird which also laid in nest 2. Black/white completely covered the eggs with straw when she left, but other females left them uncovered three times.

Nest 4. Single eggs were laid on Day 41 and 42: one could have been by Orange/blue, but whoever laid them was considered to have discontinued after Day 42. White/blue, who subsequently incubated this nest, was present on Day 1. By Day 34 this pair were avoiding groups near the barn and violently attacking followers. The female had a pronounced egg bulge on Day 36 and began to vary her visit times. She was considered to have laid or attempted to lay in nests 1 and 2 and been excluded from them in turn when incubation started on Days 45 and 47. White/blue and Orange/blue visited nest 4 on Day 47 and were considered responsible for 6 eggs laid in it up to and including Day 49. Incubation commenced on Day 50 or 51 with 8 or 9

eggs. However, laying continued and there were 20 eggs by Day 58. Between Days 45 and 58 there was frequent disturbance at the nests by intruders, but all four incubating birds withstood it.

Other nest sites and overall behaviour

Three other available sites remained unused until Day 59, even though 3 eggs were experimentally placed in one and various individuals inspected the holes. From Day 45 to 58 behaviour changed in line with normal expectations. Group display decreased and nesting pairs became even more discreet in their visits. By the end of this period, with incubation proceeding in four nests, the group had, to outward appearances, ceased associating.

The 2nd phase: Day 59 to Day 99 (29th May to 8th July)

Four new pairs were near the barn on Day 60. This increased to ten new pairs by Day 63. There was a resurgence of group display and groups again gathered in and around the barn, e.g. 18 birds on the stack on Day 63. Visits to nest holes increased again and much of the behaviour was similar to the aimless hole visiting of non-breeders. Activity was complex because another sequence of behaviour through prospecting to incubation was superimposed on a group already incubating.

The most significant events were:-

(i) Incubation continued in nests 1 to 4 inclusive. Single eggs were laid in nests 2 and 4, probably by the new birds.

(ii) Blue/yellow, incubating nest 1, was visibly disturbed. On day 63 when the pair returned at 05.44, six females were on the stack and others were nearby. Blue/yellow checked in her flight, but then continued and went into the nest. However, sometime between Days 64 and 68 she deserted. There had been no other disturbance and desertion was attributed to the new birds.

(iii) A single egg was laid in nest 5 on Day 63 with the three placed there experimentally. No further eggs were laid in this nest.

(iv) Laying started in nest 6 on Day 60; at least one of the 10 eggs was by a second female. Incubation commenced on Day 67.

(v) Seven different second phase females exhibited pronounced egg bulges on eleven occasions between Days 60 and 77 inclusive.

(vi) 11 different females were seen down-stripping away from the nest either in the pasture near the stack, or in two cases, on the stack. There were fourteen observations of this between Days 60 to 77 inclusive. All the birds except Blue/yellow were non-incubators.

(vii) From Day 74, Blue/yellow, the bird which deserted Nest 1, re-appeared in the early morning gatherings and was seen on every subsequent watch until Day 93. She continued to visit nest holes, but in an apparently aimless way, e.g. she looked in all holes except one on Day 84. She frequently "walked up", her male leading, as they had done forty days previously. On Days 74 and 77 this female was seen down-stripping near the barn.

(viii) The female incubating nest 6 was caught for ringing on Day 69. This was distinctly earlier than normal and the trauma was presumably the reason why she returned to the wrong nest! She returned to nest 1 and continued to sit until the straw was re-stacked on Day 99. In the hand this female showed traces of immature plumage, having 3 mm grey tips to the innermost greater coverts.

(ix) Clutches in nests 2, 3 and 4 hatched, nests 3 and 4 on Days 79 and 80, with hatching successes of 81, 69 and 50%.

Laying and hatching success

Since the average single clutch size is 9, an output of 171 eggs might have been expected from 19 pairs. Actually a total of 81 was laid: 66 in the first phase and 15 in the second.

Output was thus 0.47 of theoretical potential, or approximately 0.81 for the first phase and 0.17 for the second. Possibly interactions and disturbance could depress individual's performance, but analysis of nests visits and behaviour suggested that any depression in laying by experienced birds was marginal. The first five pairs in Table 5 were in the first phase which contained four further pairs, two of which were

considered experienced. The second influx birds were considered predominantly inexperienced. Overall, it was considered that 9 pairs were experienced and 10 inexperienced. At its simplest, these females could have produced the observed total if the former had laid clutches of 8 eggs and the latter one egg each. In actuality, one or two experienced birds probably laid less than average clutches, e.g. Orange/blue, whilst some inexperienced birds laid more than one egg, e.g. Yellow/red. Some of the latter may have been completely inhibited, or incapable of laying eggs.

Overall hatching success was low at 39.5% or 1.68 ducklings per pair. Failure of nest 6 could be considered a result of the observer's interference. It it had hatched completely, the figures would have been 52% and 2.2 ducklings per pair.

Discussion

Distribution and dispersion

Most breeding populations undoubtedly originated on estuarine shores, using the mud for territory and later colonising adjacent lowlands for nesting. Similar populations seen today are confined to narrow coastal strips in estuaries and do not nest inland (Patterson pers. comm. for the Ythan).

The Medway estuary, adjoining Sheppey to the west, is an area of extensive tidal ooze, broken saltings and islands. Reclamation and inundation has occurred periodically since Roman times, but some islands were last re-embanked in the nineteenth century. In the less isolated parts, Shelduck nest under small shrubs and brambles *Rubus fruticosus*, but more striking are the open nests which occur on the islands. These are in long grass, often on, or at the base of, broken sea walls and they have no top cover. The islands were remote until 20/30 years ago and even now are not frequently visited. Soft mud, deep creeks and fast currents provided security from predators, particularly Man and this is clearly the reason for the adaptation's success. The nearest to open nests known on Sheppey were those of birds which nested in barbed wire entanglements left on saltings after the last war. These were virtually open, but impossible to reach; examples were known until 1964.

Some Medway breeders have also developed the behaviour of nesting outside the area and fly 9 – 10 km inland to nest in woods. It has not been proved that these birds hold territory in the estuary, but that is the very strong presumption.

Nesting away from the shore is widespread on Sheppey; in this case the birds have been proved to hold territory on and near the shore as well as along fleets and elswhere. The use of nearby fresh water appears to be the only adaptation developed for expansion of territorial areas. It is maintained that shortage of territorial habitat is a general ecological limitation in estuaries and that to overcome this constraint the species needs the impetus of a habitat modification, as occurred in North Kent. On Sheppey territories now occur on quite small ditches, fleets and pools. From 1984, territories were recorded on two fresh water "floods" created in the RSPB reserve in 1980 and 1983.

In North Kent and Sheppey in particular, it appears that nest sites have long been a further constraint. This is supported by the immediacy with which artificial or improved natural sites are used, and the exploitation of short lived opportunities like temporary hay and straw stacks, shooting blinds, even household and building debris scattered by the 1953 sea floods. Multiple nesting may overcome nest site shortage to a certain extent, but if nesting becomes too dense, hatching will suffer.

Thus territorial and nesting behaviour are also major dispersionary factors. The relatively fixed locations of communes confirms that information is indeed effectively passed to succeeding generations, particularly as none of the 60 females colour ringed in the sixties were seen in communes during the eighties. It is believed that information transfer is facilitated by the tendency of inexperienced birds to follow experienced birds during the sequence of behavioural phases leading to laying. In the long run, efforts by experienced pairs in the communes to find isolated nest sites will lead to further dispersion until, as on Sheppey, all the available area is used. Possibly as the population approaches this stage, or after, birds able to accept a diet change may pioneer distinctly different locations. The well known, but limited, instances of inland breeding in Britain may have this origin.

Attaining laying condition

One purpose served by communes is thought to be the attaining of laying condition: for experienced pairs, single nesting would appear advantageous, but only approximately half the breeding population achieved it in 7 of 10 breeding seasons. In one year only about one quarter achieved it, Table 3. Pienkowski and Evans (1982) reported similar results from Aberlady Bay where between one half and two thirds used single nests. Nest site prospecting by single pairs was frequently observed, but only after they had associated in communes.

For the commune studied in detail, 23 days elapsed before any bird visited the nest site and another ten days before an egg was laid: both periods were after territory had been occupied. Such periods are normal.

Proximate factors may take this long to result in final breeding condition in Shelduck, but the initial period in the commune is still considered to serve the function of stimulating final growth of gonads and other glandular action (e.g. see Phillips *et al.* 1985). But the groups of birds signal the locality of nesting sites to others. Groups form every morning and persist for some hours: these are detected and joined by inexperienced birds. So in preparing for laying in this way, experienced birds reduce their chances of single nesting.

Egg laying by young breeders

The existence of young adults in the communes has been demonstrated. The appearance of egg bulges and the disappearance of these after nest visits by inexperienced birds showed that these individuals did lay. "Young" is used here to describe first time breeders: these are at least 2 years old and possibly up to 4/5 years. When multiple nesting was studied closely, it was the experienced birds which laid most of the eggs and it was they who incubated in four out of five cases.

Recognising the young adults is only part of the difficulty. There is no hard evidence on the number of eggs they lay, whether they usually incubate, the age of full maturity or if young birds increase their output of eggs from the first laying season to maturity. The Sheppey studies showed that when groups which include inexperienced birds are involved at multiple nests, many single eggs are laid. The group studied in detail illustrated this graphically at those isolated multiple nests which involved large numbers of birds, e.g. 10 and 12 pairs or more. In these, large numbers of eggs, for example, 4 and 6 per day, would be deposited for one or sometimes two days only, during a laying period of normal length. Many females in these groups were considered inexperienced and in a few cases such birds were proved to have laid single eggs in or near clutches.

However, some 28% of a sample of 72 incubating females had traces of immature plumage on their greater coverts. There is strong presumption that these birds had not reached full maturity. Such birds were sometimes found on small clutches, but no more frequently than birds in mature plumage. Nevertheless support is lent to the proposition that some young birds, probably the older ones, can lay more than one egg and can incubate in certain circumstances.

The precise age of these young adults remains uncertain. It is known that 2 year old birds lay in captivity (Hori 1964), but detailed information on clutch size and incubation are not available. At Aberlady Bay, the youngest female seen with a brood was aged four, from a sample of 52 ringed ducklings (Pienkowski and Evans 1982b).

On Sheppey it has always been maintained that two year old females can breed but in common with other studies the extent has remained unknown. If young first time breeders can acquire territory at approximately the same time as experienced birds, they follow the latter to commune areas at normal dates and become involved in multiple nesting to varying extents. Some, possibly the youngest, will lay only 1 egg, but others, probably older, may be capable of laying more.

Multiple nesting

On the scale recorded in 1985 and 1986 and at the density seen in the closely studied commune, multiple nesting might easily be taken as entirely disruptive. However, in the sixties, at very different density levels, hatching success was at times higher than in single nesting (Hori 1964). Pienkowski and Evans (1982 b) reported opposite results in a dune nesting community at Aberlady Bay. The present work suggests that the outcome is variable and density dependent.

In years of high duckling output, e.g.

1963 and to a lesser extent 1985, the presence of inexperienced birds was often difficult to detect at inland and upland communes. In such years, after preliminary association in communes, pairs separated and prospected in relative isolation. Later examination of nests showed that some multiple nesting had occurred. If a commune consisted entirely of pairs having experienced females, in an area without nest site shortage, multiple nesting would be expected to occur unusually and then by accident.

Denser conditions are actually normal and communes can consist of pairs with females from two years old to maturity. Many birds, considered young adults, deliberately lay in the nests of others. This behaviour has been described as nest parasitism, but although this may be terminologically correct, it can no longer be considered appropriate. In Shelduck, it does not have the adaptive significance postulated for brood parasites generally (see Perrins and Birkhead 1983).

The central postulate here is that multiple nesting is a behavioural adaptation by which females in their first year of laying are introduced to secure nesting sites, and the small number of eggs that they lay are incubated, generally by more experienced birds. This postulate is also supported by the high tolerance which experienced females exhibit to the resulting disturbance, and the generally passive acceptance of large clutches.

Outcomes of multiple nesting are seen as a cline, from success at low densities, to total failure at high density. The five multiple nests in the closely studied commune illustrate dense nesting conditions and the resultant deterioration of hatching success. Although the total of nests examined was substantial, annual samples were small. This was unfortunate because it is the variation in annual figures which is important in terms of the postulates made. Up to 62% of eggs laid were in multiple nests whilst hatching success varied between 27% and 95% over the years. Clearly if the samples represent the breeding populations accurately, the effects on duckling output would be extremely important.

Down-stripping away from the nest

This behaviour was described previously and attributed to failed nesters (Hori 1964 and 1969). Females were found to behave in this way in three circumstances. (i) Experienced adults whose nest had failed. (ii) Experienced adults who had competed for multiple nests, but been excluded from incubating by other birds. (iii) Young females, laying or trying to lay in multiple nests, possibly for the first time, when excluded by incubating birds.

The overall conclusion is that females capable of laying grow down patches which are plucked at the onset of incubation to make a cover for the clutch. Down-stripping away from the nest occurs when females do not have a clutch to cover, either because a nest fails, or because of the circumstances of multiple nesting. Most of this activity is considered to be by young females, and as a corollary of multiple nesting.

Regulation of population

The behaviour and nest studies lead to the further hypothesis that commune association through multiple nesting achieves regulation in the breeding population. The extent to which this effects the overall population, in an area where recruitment is possible from a large winter population and from similar nearby populations, does not affect the issues discussed here. This hypothesis was proposed previously (Hori 1969), but further study suggests that it operates in an entirely different manner to that then suggested. It now seems that the number of young adult females, a very direct predictor of the breeding population's future potential, is the controlling variable. Following tendencies lead these females to communes where some potential first time breeders experience new habitat in the uplands. Many will have experienced the holes in trees and stacks once, for some hours, when they were ducklings. Some may not have experienced them at all. Their activity at multiple nests, which in itself assists the learning of hole nesting behaviour and provides for incubation of fertile eggs laid by them, causes variation in hatching success. The status of such females has yet to be clarified. Patterson (1982) showed that only 40% of 2 year old females on the Ythan held territory. Also, there was no evidence that Shelducks without territory ever lay eggs (Young 1964; Williams 1973; Patterson *et al.* 1974). It seems most likely that young females which have terri-

tories are those which participate in communes proper and that young pairs without territory come later. Most or all of the second phase birds in the closely studied commune could have been of the latter status. On the Ythan, Williams (1973) determined that whereas territorial adults made up the bulk of birds visiting nesting areas at the April peak, the peak in May and June included two and three year olds without territories.

When the number of young adults is low, interference at nests is tolerable and hatching success high. Conversely, when the proportion rises, their activity in the communes' multiple nests progressively reduces hatching success. The ultimate limit is probably dump nesting.

Experienced birds were shown to have developed remarkable behaviour to enable egg laying and incubation to continue despite high levels of intra-specifc interference. Four experienced females managed to reach the incubation stage by employing stealth and aggression, by disguising their activities, by covering eggs, by varying their visit times or watching for opportunities to reach the nests unobserved, by having exceptional tolerance of disturbance, and in two cases changing nest sites.

The loss of trees in the area involved more than the loss of one quarter of the nest sites (Hori 1964). Seclusion, which most of the upland communes had in the sixties, was also lost and small groups could no longer virtually disappear. Assemblies of such conspicuously coloured birds could be detected at long range in the treeless landscape, even at ground level. In many of these it was more difficult for experienced birds to elude others when prospecting, laying and incubating.

The combination of habitat change and high population level considerably increased density in the communes of the eighties. This was considered responsible for the widely different hatching success particularly in 1985 and 1986. Because of the difficulty of nest study in this species only small samples of multiple nest histories have been published. One consequence has been a tendency to combine annual hatching success data over several years. This may have obscured the significance of annual variation, which would be expected if the regulation hypothesis is correct. Larger annual samples will be necessary to confirm the postulates advanced. Detecting regulation in the field is problematic, but limited support is seen in the overall population statistics in Table 6. It should be noted that the summer populations in 1959/61 were 220, 250, 270.

The immediate increase in duckling output following exceptionally severe winters has been noted previously (Hori 1969). This occurred twice; in 1963 and again in 1985. On both occasions the preceding severe winter caused heavy mortality. There was no measurable increase in average clutch size, but the percentage of total eggs laid in multiple nests was high in both years (Table 3) as was the hatching success (Table 4). The presumption is that winter mortality removed significant numbers of young adult females. There is further weak support in the sixties' data. When the large duckling output of 1963 had worked its way through to the breeding population, and 2 and 3 year old birds swelled the breeding populations in 1965 and 1966, duckling output per pair of the breeding population was the lowest recorded. On the Ythan, "hatching success, fledging success and the number of young fledged per territorial pair all decreased significantly with increasing numbers of territorial pairs in the population" (Patterson 1982).

The regulation postulate above, is, of course, a density dependent mechanism, but the manner of operation does not seem to have been previously suggested in birds.

Table 6. Summer population statistics.

	1962	63	64	65	66	67	68	84	85	86
Total birds	260	245	390	465	495			712	630	690
Breeding pairs	70	73	65	115	147			150	155	169
Non-breeding birds	120	99	260	235	201			412	320	352
Ducklings on nursery water	245	515	243	285	244			349	548	327
Ducklings/pair	3.5	7.1	3.5	2.5	1.7			2.3	3.5	1.9

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Summary

A breeding population of Common Shelduck *Tadorna tadorna* was re-studied after an interval of sixteen years.

Generally distribution is limited by narrow territorial preference, but given habitat modification, adaptation can relieve this constraint. Dispersion is effected by territorial and commune behaviour. Communes provide information transfer on nesting locations and experience on hole nesting, stimulate achievement of breeding condition, and, through multiple nesting, regulate breeding output. Communes involve experienced and inexperienced birds. The latter are probably aged from two to four years and many, probably the youngest, lay only small numbers of eggs, sometimes one.

Only a fraction of the population used single nests. Increased density in the 1980s resulted from a larger population and habit changes. This caused different outcomes from multiple nesting. It is hypothesized that behaviour of inexperienced adult females at multiple nests causes density dependent regulation by varying hatching success. Most young females may not be capable of incubating. At low densities multiple nests could provide for incubation of their eggs at success rates comparable with or greater than single nests. At high densities the activity of young females is disruptive and can cause total failure.

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